

# Oceanography and Marine Biology

## An Annual Review, Volume 61

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First published 2023

ISBN: 978-1-032-42696-9 (hbk)

ISBN: 978-1-032-54845-6 (pbk)

ISBN: 978-1-003-36387-3 (ebk)

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DOI: 10.1201/9781003363873-3

The funder for this chapter University of Sydney



**CRC Press**

Taylor & Francis Group

Boca Raton London New York

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Taylor & Francis Group, an **informa** business

## SURVIVING THE ANTHROPOCENE: THE RESILIENCE OF MARINE ANIMALS TO CLIMATE CHANGE

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**Abstract** If marine organisms are to persist through the Anthropocene, they will need to be resilient, but what is resilience, and can resilience of marine organisms build within a single lifetime or over generations? The aim of this review is to evaluate the resilience capacity of marine animals in a time of unprecedented global climate change. Resilience is the capacity of an ecosystem, society, or organism to recover from stress. Marine organisms can build resilience to climate change through phenotypic plasticity or adaptation. Phenotypic plasticity involves phenotypic changes in physiology, morphology, or behaviour which improve the response of an organism in a new environment without altering their genotype. Adaptation is an evolutionary longer process, occurring over many generations and involves the selection of tolerant genotypes which shift the average phenotype within a population towards the fitness peak. Research on resilience of marine organisms has concentrated on responses to specific species and single climate change stressors. It is unknown whether phenotypic plasticity and adaptation of marine organisms including molluscs, echinoderms, polychaetes, crustaceans, corals, and fish will be rapid enough for the pace of climate change.

**Keywords:** Anthropocene; Phenotypic Plasticity; Resilience; Transgenerational Plasticity; Ocean Warming; Ocean Acidification; Marine Organisms; Adaptive Capacity

## Introduction

We are in the age of the Anthropocene. Human-induced elevations in anthropogenic carbon dioxide ( $\text{CO}_2$ ) are warming and acidifying oceans across the globe. The rate of change is unprecedented on geological timescales (Collins et al. 2013, Lee et al. 2021) and is predicted to severely impact marine animals across all life-cycle stages and habitats (Kroeker et al. 2013, Byrne 2011, Ross et al. 2011, Przeslawski et al. 2012, Gazeau et al. 2013, Parker et al. 2013, Poloczanska et al. 2013, Byrne & Przeslawski 2013, Ross & Adam 2013, Przeslawski et al. 2015), although there continues to be debate about variation in responses (Hendriks et al. 2010, Gazeau et al. 2013; Figuerola et al. 2021) and the extent of marine organisms and life stages impacted (Leung et al. 2022). Climate models project that, by the end of this century, ocean acidification (OA) will be *virtually certain*, and depending on the shared socioeconomic pathway (SSP), surface ocean pH levels will decrease from the mean pH in 1950 by 0.1 unit in the best-case scenario (SSP1) to 0.45 pH units in the worst case scenario (SSP5-8.5). Ocean warming (OW) will also occur; sea-surface temperatures (SSTs) (Lee et al. 2021) will rise by  $1.51^\circ\text{C}$  (SSP, 1–2.6 range  $1.02\text{--}2.19^\circ\text{C}$ ) to  $2.89^\circ\text{C}$  times (SSP5–8.5 range  $2.01\text{--}4.07^\circ\text{C}$ ) (Fox-Kemper et al. 2021). Increased variation in the water cycle will also occur leading to increased precipitation, freshening (i.e. reduced salinity), and greater variability in storms, changes in ocean currents, and droughts across the globe (Przeslawski et al. 2008, Scanes et al. 2020, Lee et al. 2021).

This rise in SST is being exacerbated by the increase in the frequency, intensity, and duration of Marine Heat Waves (MHWs) extreme heating events that have rapid and catastrophic consequences for marine ecosystem (Wernberg et al. 2013, Hughes et al. 2017, Hughes et al. 2019; Leggat et al. 2019, Smith et al. 2021) combined with hypoxic event (HEs) which together with OA and OW will potentially be more devastating (Oliver et al. 2018, Sampaio et al. 2021). To cope with changing ocean conditions, some marine organisms have migrated poleward (rate of  $72\text{ km decade}^{-1}$  at their leading edge) resulting in novel species interactions and population structures (Poloczanska et al. 2013).

Migration will only be successful if an organism has sufficient dispersal potential and suitable habitat for settlement. Adult migration is not possible for sessile marine organisms which rely on larval dispersal. It is increasingly apparent that if marine organisms had to persist through the Anthropocene, they will need to be resilient to multiple stressors.

Climate change stressors are likely to interact (Byrne & Przeslawski 2013). The few studies which have measured the interactions of multiple stressors, such as ocean acidification (OA), OW, and oxygen loss or hypoxia in the ocean (OD, ocean deoxygenation), have found additive, synergistic, or antagonistic effects on marine organisms (Bijma et al. 2013, Harvey et al. 2013, Gobler & Hannes 2016, Figuerola et al. 2021, Sampaio et al. 2021). Bijma et al. (2013) state that the OA, OW, and OD are the ‘deadly trio’, and in the past, such multiple stressors ‘were often coupled with extinctions of major species’ groups’.

In this three-part review, we focus on the resilience of marine animals to climate change mainly the dual major stressors of OA and OW (see Table 1). The first section defines resilience and adaptive capacity. The second section summarises the resilience of marine animals focusing on molluscs, echinoderms, polychaetes, crustaceans, corals, and fish to climate change. Finally, the third section identifies the gaps in research required to determine whether marine animals will survive in the Anthropocene.

### Definition of resilience

Definitions of resilience vary depending on the context and discipline in which resilience is applied. However, resilience is broadly defined as the capacity of system, i.e., an ecosystem, society, organism, or individual, to ‘bounce back’, maintain the same structure, functioning, and identity, and persist after responding or recovering from a disturbance or stress (Harrison 1979, Holling 1996, Nyström et al. 2000, Carpenter et al. 2001, Holling & Gunderson 2002, Folke et al. 2004, Bernhardt & Leslie

**Table 1** Glossary of terms used to describe responses of marine animals to climate change

Term	Definition
Acclimation	The adjustment of an organism to experimental conditions in the laboratory without an adjustment in their genetics. Acclimation has been used to describe phenotypically plastic responses of organisms generated under controlled laboratory and experimental manipulations when the factor of interest can be isolated.
Acclimatisation	The adjustment of an organism to environmental conditions in the field or environment rather than the laboratory without an adjustment in their genetics. Acclimatisation has been used to describe phenotypically plastic responses in natural conditions.
Adaptation	The evolutionary mechanism where natural selection of traits is genetically passed on, typically over many generations, to create an organism suited to the environment.
Adaptive capacity	The capacity of the ecosystem or organism to improve and reorganise in response to stress such as climate change through phenotypic plasticity (acclimation, acclimatisation) or adaptation, distributional shifts, and rapid evolution of traits suited to new conditions.
Epigenetics	The modification of phenotype plasticity of an organism through altered gene expression without an alteration to the DNA sequence. 'Epi' means above the DNA and includes DNA methylation, modification of histones, and non-coding RNA.
Fecundity	The maximum physiological potential reproductive output of an organism to produce offspring (reproductive output). This differs from fertility, which is the number of offspring born.
Genotype	The genetic characteristics of an organism.
Hypoxia (Ocean Deoxygenation, OD)	Low or depleted oxygen in marine ecosystems. This can occur when algal growth and oxygen consumption in respiration exceed photosynthesis and oxygen production. Oxygen loss or hypoxia in the ocean has been shortened to OD, ocean deoxygenation and hypoxic events to HEs.
Multiple stressors	Multiple disturbances or impacts that combine to cause stress on an organism, i.e., ocean acidification, ocean warming, decreased salinity, hypoxia, and inadequate food. Disturbances rarely occur in isolation and often combine as double or triple disturbances being additive, synergistic, or antagonistic. Additive is when the combined effect is equal to the sum of separate stressors. Synergistic is when multiple stressors combine to be greater than an additive effective. Antagonistic is when multiple stressors combine to be less than an additive effect.
Ocean acidification (OA)	Oceans absorb 25–50% of excess CO <sub>2</sub> caused by greenhouse gas emission in the atmosphere as a result of burning fossil fuels. IPCC report suggests that oceans will acidify and pH levels will decrease by 0.1–0.45 pH units depending on the shared socioeconomic pathway (SSP) from a mean pH in 1950 of 8.1. Ocean acidification has been shortened to OA.
Ocean warming (OW)	Oceans absorb between 25–30% of excess heat caused by greenhouse gas emissions in the atmosphere as a result of burning fossil fuels. IPCC reports suggest that sea-surface temperatures (SSTs) will rise by 1.51 to 2.89°C times depending on the SSP by 2100. Ocean warming has been shortened to OW.

*(Continued)*

**Table 1 (Continued)** Glossary of terms used to describe responses of marine animals to climate change

Term	Definition
Persistence	The continuation of an ecosystem, society, or organism to retain the same identity through the processes of resilience or resistance.
Phenotype	The physical or morphological characteristics of an organism.
Phenotypic plasticity	The capacity of a marine organism and genotype to produce more than one phenotype and adjust their behaviour or physiology when exposed to different environments. Plasticity can either be adaptive (persistence in a new environment) or be nonadaptive (away from optimum).
Resilience	The capacity of an ecosystem, society, or organism to absorb disturbance and reorganise while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks. Resilience reflects the degree to which a complex adaptive system is determined by its capacity to reorganise and adapt in order to avoid being disturbed again.
Resistance	The response of an ecosystem, society, or organism to absorb high levels of disturbance or stress without visible response to the disturbance.
Selective breeding	The process where an organism is bred for traits, also known as artificial selection.
Stressors	Disturbance or impact that causes stress on an organism, i.e., ocean acidification, ocean warming, decreased salinity, hypoxia, and inadequate food.
Trade-off	The adaptive traits favoured for one or more conditions lead to reduced performance in another unselected trait.
Threshold	The boundaries of resilience. When an ecosystem, society, or organism is close to a threshold, a small amount of stress can breach the threshold and tip the system or individual over to an alternate state or individual collapse. These alternate states are difficult to reverse.
Tipping point	The limits of resilience are ‘tipping points’. Tipping points are reached when the cumulative effect of stress and challenges or large and traumatic events does not build resilience, is counterproductive, and tips over a threshold of tolerance to an alternate state.
Transgenerational effects	The phenotype and/or patterns of gene expression that are passed from one generation to the next which do not create changes to the DNA sequence.
Transgenerational plasticity (TGP)	The transmission of information from one generation to the next, i.e., across generations, which results in phenotypic changes to offspring without an alteration to DNA in response to the environmental stress experienced by one or both parents. Transgenerational effects can be adaptive, resulting in pre-adapted offspring that have traits with increased fitness because of the environmental conditions experienced by their parents.

2013, Walker et al. 2004, Walker 2019). Walker (2019) states that resilience of a system is the capacity to absorb the disturbance or stress and reorganise while undergoing change so as to retain essentially the same function, structure, feedbacks, and most importantly, retain identity. Critically, resilience is not only ‘bouncing back’ but also the degree to which a complex adaptive system can learn, reorganise, and adapt (while retaining the same functions and identity) to avoid being disturbed again (Gunderson 2000, Walker et al. 2004, Adger et al. 2005, Walker 2019, Table 1). This capacity to learn is the component of resilience called ‘adaptive capacity’ (Holling & Gunderson 2002, Walker 2019).

Critical to resilience is that the system must retain those traits that made that system unique, its identity, function, or even appearance (Carpenter et al. 2001, Adger et al. 2005, Walker 2019). If a system reorganises and loses its identity, then there is no resilience. In this way, resilience recognises that systems are capable of reorganising and building capacity to adapt to change perhaps as alternative stable states that retain the same controls on function and structure (Holling 1996) but may not exactly be the same (Gunderson 2000, Walker et al. 2004, Walker 2019). Walker (2019) also cautions on the misconceptions that resilience is simply the capacity to ‘bounce back’ or that it is always being thought of as desirable trait because resilience is also the capacity to “learn” and there are undesirable resilient systems such as algal colonised coral reefs.

Persistence is a key aspect of resilience. If an ecosystem or an organism can no longer persist and ceases to exist, then resilience cannot exist (Holling & Gunderson 2002). Persistence can also be achieved through resistance. Some systems are capable of absorbing high levels of external pressure without experiencing a measurable disturbance and are therefore considered resistant (Table 1). Resistance has been considered a complimentary attribute of resilience (Carpenter et al. 2001) and sometimes resistance is distinguished from resilience (Lake 2013, Connell et al. 2016).

Finally, preventing change does not improve resilience. Counter-intuitively, change improves resilience, i.e., probing at the thresholds or tipping points improves resilience and is a safe change (Walker 2019, Table 1). Resilience is a common mechanism by which systems persist and is often observed in biological systems (Holling 1996, Gunderson 2000, Nyström et al. 2000, Carpenter et al. 2001, Holling & Gunderson 2002, Walker 2019).

Ecological resilience theory is often applied to marine ecosystems (Bernhardt & Leslie 2013), such as coral reefs (Hughes et al. 2010, 2017). Hughes et al. (2010) outlined a concept of ecosystem resilience that is defined by non-linear threshold dynamics in response to slow and fast drivers of change, alternate persistent phases, reinforcing feedbacks, and hysteresis. This concept emphasises the difference between slow stressors, such as increasing ocean temperatures, and fast stressors, such as a cyclone, which, when combined, can cause coral reefs to exceed thresholds and shift from coral-dominated to algae-dominated systems. Coral reefs are an ecosystem in crisis due to global warming and a range of human activities that have reduced their capacity for resilience through habitat fragmentation and reduction of species and functional diversity (Nyström et al. 2000, Hughes et al. 2017). The non-linearity of responses to stress is not only evidenced in marine ecosystems but can also be observed in marine organisms. This review is novel because it focuses on the responses of marine animals to climate change rather than exploring properties and processes that enhance resilience of marine ecosystems (Bernhardt & Leslie 2013). By understanding the resilience of marine organisms, we may be better able to understand how marine animals and single species dominated ecosystems (e.g., oyster reefs) will persist in response to global climate change (Munday et al. 2013a).

Importantly, when defining or measuring resilience, there needs to be a timescale relative to the issue that is under investigation (Carpenter et al. 2001). In this review, we utilised the year of 2100 as a reference point within the Anthropocene for the impacts of climate change (Collins et al. 2013, Lee et al. 2021), as per the IPCC reports (Collins et al. 2013, Lee et al. 2021, Fox-Kemper et al. 2021) and broader climate change literature.

### *Adaptive capacity of marine organisms*

The adaptive capacity of marine organisms in response to climate change is the capacity of an ecosystem, society, and organisms to learn or improve in response to disturbance or stress and take advantage of opportunities for change (Bernhardt & Leslie 2013, Hughes et al. 2017, Table 1). Adaptive capacity can occur through phenotypic plasticity (acclimation or acclimatisation), adaptation (genetic diversity), and distributional shifts (Reusch 2014, Bernhardt & Leslie 2013, Reid & Whitehead 2016). Phenotypic plasticity is the capacity of a marine organism and genotype to produce more than one phenotype and adjust physiology, morphology, or behaviour

which improve the response of an organism in a new environment without altering their genotype (Munday et al. 2019, Table 1). While acclimation is reserved for adaptations generated under controlled laboratory experiments when the factor of interest can be isolated, acclimatisation refers to adaptations in response to fluctuations in natural conditions (Table 1). Although there have been arguments for the separation of acclimation and acclimatisation, which some authors argue is the ‘cause of considerable confusion and logically meaningless’ (Munday 2014), it is likely that there are different mechanisms driving responses of marine organisms in laboratory and field experiments, and thus, in this review, these two components of phenotypic plasticity have been described separately.

Phenotypic plasticity can allow organisms to build resilience to stress quickly, both within and across generations. Plasticity can occur within a generation, across a generation, and across multiple generations known as transgenerational plasticity (TGP) (Ross et al. 2016, Byrne et al. 2020, Table 1). Phenotypic plasticity is also a rapid response mechanism which may buffer populations against the impacts of climate change and provide the time necessary for genetic adaptation to occur. There can be costs and limits of phenotypic plasticity where an improvement in a characteristic or trait can result in a trade-off in another, which have the capacity to severely limit the fitness and survival of a species (Calosi et al. 2016, Chakravarti et al. 2016, Kelly et al. 2016, Collins et al. 2020, Parker et al. 2021, Table 1). For example, if an individual is better able to calcify under OA, but this resilience comes at a cost to fecundity, then this will reduce the supply of offspring and recruits to the next generation. There needs to be greater understanding of whether improvements in one or more traits in response to climate change can be maintained without trade-offs in other traits that ultimately limit the fitness, survival, and success of marine organisms (Calosi et al. 2016, Chakravarti et al. 2016, Kelly et al. 2016).

The duration of phenotypic plasticity, and hence, its benefit in a constantly changing ocean is also not well understood. However, it is important to note that phenotypic plasticity may hinder adaptation. In contrast to phenotypic plasticity, adaptation is typically a longer process that occurs over many generations and involves the selection of tolerant genotypes which shifts the average population phenotype towards the fitness peak. Assessing the adaptive capacity of marine species over this century is somewhat difficult as many species possess long generation times and/or are challenging to maintain in the laboratory.

In this review, we synthesise the responses and resilience of the major groups of marine animals including shelled molluscs, echinoderms, polychaetes, corals, crustaceans, and fish to climate change with a focus on ocean warming and acidification. We define resilience as the adaptive capacity of marine animals to improve key physiological, morphological, and/or behavioural traits that are known to be impacted by climate change. Further, we explore potential adaptive capacities of marine animals which have been explored to date to change through phenotypic plasticity or adaptation to near-future ocean acidification. Finally, we summarise the main challenges for the survival of marine animals in the Anthropocene.

## The resilience of marine animals

### *Shelled molluscs*

Shelled molluscs are ecologically and economically important in marine and estuarine environments. Laboratory and field studies report negative impacts of climate change on early life-history stages, growth, energy budget, immune response, acid–base balance, behaviour, and survival of mollusc species (Harvey et al. 2013, Gazeau et al. 2013, Kroeker et al. 2013, Parker et al. 2010, 2013, Lefevre 2016). Variability in responses has been observed among and within species, however, with some studies finding neutral or even positive effects of climate change on some life-history stages or traits (Hendriks et al. 2010, Figuerola et al. 2021, Leung et al. 2022).

Studies assessing the phenotypic plasticity capacity of molluscs to OA have predominantly focused on TGP. For many species, parental exposure to elevated CO<sub>2</sub> can significantly reduce the negative impacts of elevated CO<sub>2</sub> on larval, juvenile, and adult offspring (Parker et al. 2012, Ross et al. 2016, Parker et al. 2021, Lim et al. 2021, Table S1). For example, Kong et al. (2019) found that the negative effects of elevated CO<sub>2</sub> on the fertilisation, larval size, and abnormality of the mussel, *Mytilus edulis*, were reduced following parental exposure to elevated CO<sub>2</sub> (1100–2400 µatm for 4 w). Zhao et al. (2018a) found similar beneficial TGP effects in the clam, *Ruditapes philippinarum*, as juvenile shell growth decreased with elevated CO<sub>2</sub>, but this effect was no longer present when parents were exposed to elevated CO<sub>2</sub> (1000 µatm for 10 w) during reproductive conditioning. The beneficial carry-over effect observed in offspring of *R. philippinarum* was found to persist, highlighting the potentially long-lasting nature of TGP responses in molluscs to OA, possibly as a shift to more energy-efficient ion-regulatory mechanisms in the calcifying fluids of juveniles following parental exposure to elevated CO<sub>2</sub> (Zhao et al. 2017, 2018a, b).

In the Sydney rock oyster, *Saccostrea glomerata*, studies have found that TGP responses of molluscs to OA differ within a species between populations (Parker et al. 2012, 2021, Table S1). Parker et al. (2012) compared the TGP response of a wild and selectively bred population of *S. glomerata* to OA and found that, although the shell growth and development rate of both populations was improved following parental exposure to elevated CO<sub>2</sub> (856 µatm for 5w), the improvement was greatest in the selectively bred population. Transcriptomic analysis found a differential abundance in the genes associated with the control of the cell cycle and maintenance of cellular homeostasis (Goncalves et al. 2018), suggesting that the selectively bred population had improved capacity to prevent apoptosis caused by oxidative damage.

TGP responses of *S. glomerata* have also been found to depend on tidal exposure and habitat, respectively (Scanes et al. 2017, Parker et al. 2021). Despite being more resilient to OA than subtidal populations, populations of *S. glomerata* living in the high intertidal zone which experience episodes of tidal emersion (air exposure) have limited capacity to improve this resilience via transgenerational plasticity (Parker et al. 2021). It is also likely that TGP responses have carry-over energetic links (Gibbs et al. 2020, 2021a,b) and alter the microbiome (Scanes et al. 2021a,b).

Finally, for a small numbers of mollusc species studied to date, TGP to elevated CO<sub>2</sub> has led to neutral or negative impacts for offspring (Griffith & Gobler 2017, Venkataraman et al. 2019). In the clam, *Mercenaria mercenaria*, and scallop, *Argopecten irradians*, adult exposure to elevated CO<sub>2</sub> (2500 µatm for 8 w) did not improve survival and shell length of larvae, and it increased the negative impact of elevated CO<sub>2</sub> on larval metamorphosis. Collectively, these studies suggest that while shelled molluscs show great capacity for phenotypic plasticity to OA via TGP, the nature (positive, negative, or neutral) and strength of TGP responses will depend on the species, population, and habitat.

The relatively long generation times of many mollusc species makes assessing their capacity for genetic adaptation to OA over multiple generations difficult (Thomsen et al. 2017). Consequently, adaptive capacity in molluscs has been investigated by examining local adaptation – where populations are experiencing naturally high CO<sub>2</sub> (Johannesson et al. 2011, De Wit & Palumbi 2013, Thomsen et al. 2017). For example, in Kiel Fjord in the western Baltic Sea populations of the mussel, *Mytilus edulis* experience episodes of low pH and elevated CO<sub>2</sub> during their summer reproductive season. Thomsen et al. (2017) used a common garden experiment to compare responses of *M. edulis* populations from Kiel Fjord with that of a population collected from the North Sea, where pH and CO<sub>2</sub> are less variable. They found larvae from Kiel Fjord were better adapted to elevated CO<sub>2</sub> (2400 µatm) with greater shell growth and survival than larvae from the North Sea population at elevated CO<sub>2</sub>.

The adaptive capacity of mollusc populations to OA has also been measured through assessment of tolerant genotypes (Parker et al. 2011, Fitzer et al. 2018, Stapp et al. 2018, Spencer et al. 2020). Stapp et al. (2018), for example, created genetically distinct family lines of the mussel, *M. edulis*, by crossing eight single dam-sires from a mussel population collected from Kiel Fjord in the Baltic Sea. After exposure to elevated CO<sub>2</sub> (2400 µatm) during larval development, for some family lines, there

was close to 100% mortality of larvae prior to settlement, while other families were more tolerant and successfully settled at elevated CO<sub>2</sub>. Family lines of the Sydney rock oyster, *Saccostrea glomerata*, also varied in their response to elevated CO<sub>2</sub>. Parker et al. (2011) exposed juveniles of 10 family lines of *S. glomerata* to elevated CO<sub>2</sub> (1000 µatm) for 4 days following settlement. In eight out of 10 family lines, shell growth decreased with exposure to elevated CO<sub>2</sub>, but in two family lines, shell growth was not significantly affected. Fitzer et al. (2018) also found family lines of adult *S. glomerata* selected to grow faster and have resistance to disease had increased order in the crystallography of their shell compared to wild oysters.

Historically, studies which assessed the phenotypic plasticity and adaptation capacity of molluscs to temperature have focused largely on temperature within their current thermal range (i.e., across their vertical and latitudinal distribution). Comparatively and surprisingly, however, our understanding of the phenotypic plasticity and adaptation capacity of molluscs to future warming oceans is largely in its infancy, particularly for populations living close to their upper thermal limit. General trends suggest that the capacity for molluscs to acclimate and adapt to OW will be species specific. A study by Pereira et al. (2020), for example, found that acute exposure to heat stress (+6–8°C for 24 hours) improved the long-term survival of adults of the flat oyster, *Ostrea angasi*, but not those of the Sydney rock oyster, *S. glomerata*, when transferred to OW conditions (+4.38°C above ambient) in the field. The capacity for molluscs to acclimate and adapt to OW will also depend on where in the species' thermal tolerance range the population is located. Populations inhabiting low to mid positions of their thermal tolerance range will likely have greater capacity for phenotypic plasticity or adaptation to OW than those inhabiting the upper position of this range (Stillman 2002, Somero 2010, Tomanek 2010). For example, cold-adapted populations of the intertidal marine snail, *Chlorostoma funebralis*, collected from Northern California (USA), had greater than 50% survival when exposed to acute heat stress of 39°C, which is 4°C above the current maximum temperature they experience in the field (Gleason & Burton 2013). In comparison, warm-adapted populations collected from Southern California (USA) suffered 100% mortality at 41°C, a temperature which could be experienced in the field. The authors suggested that the warm-adapted populations are living close to their upper thermal limit and have limited capacity for phenotypic plasticity to OW (Gleason & Burton 2013). The studies that have considered the TGP response of shelled molluscs to OW have found negative responses. For example, when adults of the limpet *Siphonaria australis* were exposed to elevated temperature (25°C for 4w) compared to ambient temperature 16°C, the size of newly hatched larvae when reared for 24 hours and the viability of embryos at elevated temperature were reduced (Kessel & Phillips 2018). Based on the limited evidence available, it appears that the capacity of shelled molluscs to build resilience to OW may be limited, especially for molluscs living close to their upper thermal limit or in areas which are warming rapidly (Scanes et al. 2020).

### *Echinoderms*

The impacts of OA and OW as well as the interactions between these stressors across echinoderm life stages (gametes to adults) and a broad range of traits (genes/cells to whole organism physiology) have been investigated in many studies, with most research on sea urchins (Byrne 2012, Dubois 2014, Evans & Watson-Wynn 2014, Foo & Byrne 2016, 2017, Byrne et al. 2018, Byrne & Hernández 2020). Research on impacts of marine heatwaves is also emerging (Balogh & Byrne 2020, Gall et al. 2021, Minuti et al. 2021, 2022). Importantly, increased precipitation (i.e., reduced salinity) is particularly deleterious to echinoderms across all life stages (e.g., Russell 2013, Clements et al. 2022, Table S1).

In general, acidification stunts growth of adults and calcifying larvae (Byrne et al. 2013a, b), whereas warming can stunt growth of adults and both calcifying and non-calcifying larvae, reflecting the temperature-size rule (Nguyen et al. 2012, Karelitz et al. 2017, Dworjanyn & Byrne 2018, Balogh & Byrne 2020) as well as reducing scope for growth due to the diversion of energy to acid/base regulation (Stumpf et al. 2011, 2012). For OA and OW as single stressors, amelioration

of impacts can be achieved with provision of excess food (Wangensteen et al. 2013, Foo et al. 2020). However, for some species trade-offs in the presence of smaller larvae, juveniles and adults remained (Wangensteen et al. 2013, Dworjanyn & Byrne 2018). In multistressor studies, warming within tolerance ranges can ameliorate the impact of acidification on calcification and growth (Byrne & Hernández 2020). It is well known that parental exposure can dramatically shift the tolerance of echinoderm progeny (Byrne 2011) and has been investigated in experiments where urchins were maintained in warming, acidification, and multistressor conditions before using their gametes to generate progeny (Table S1).

Natural proxies of acidification conditions such as upwelling zones, estuarine gradients, and CO<sub>2</sub> vents show the potential in sea urchins for climate adaptation through phenotypic adjustment and/or beneficial genetic selection. Populations of *Strongylocentrotus purpuratus* in the California Current upwelling system have experienced low pH conditions for thousands of years and their reproductive biology may be genetically adapted to low pH (Pespeni et al. 2013a,b, Gaitán-Espitia et al. 2017). The offspring of *S. purpuratus* from the upwelling system living in higher CO<sub>2</sub> conditions are more tolerant of acidification than the offspring of parents from non-upwelling conditions with only a slight decrease in growth at pH 7.7 (Kelly et al. 2013). In a reciprocal breeding experiment with parents from high and low CO<sub>2</sub> sites, the impact of acidification on larvae was lower if the mother originated from the high CO<sub>2</sub> site, indicating phenotypic plasticity (Kelly et al. 2013). Similarly, the larvae of *Paracentrotus lividus* from tide pools that have low night-time pH (pH 7.4) are more robust to reduced seawater pH (Moulin et al. 2011). In contrast, the offspring of *Echinometra* sp. from a vent site reared in acidification conditions showed the same stunted development as larvae of non-vent urchins (Lamare et al. 2016) suggesting no positive effects of parental acclimatisation on larval growth.

Sea urchins living at CO<sub>2</sub> vents show considerable tolerance for acidification. *Arbacia lixula*, *Paracentrotus lividus* and *Echinometra* sp. can tolerate low pH conditions at vents and can even outperform conspecifics from ambient pH sites (Calosi et al. 2013, Collard et al. 2016, Uthicke et al. 2016, Foo et al. 2018a). Physiological mechanisms and indirect ecological effects (more food at vent sites) may determine the presence of sea urchins in future ocean conditions. It appears that a mean pH<sub>T</sub> 7.8 approximates the lower level of acidification for sea urchins to survive and succeed at CO<sub>2</sub> vents (Calosi et al. 2013, González-Delgado & Hernández 2018), although at some of these sites pH can experience acidification to pH<sub>NBS</sub> 6.9 (Foo et al. 2018b).

*Paracentrotus lividus* resident in vent conditions exhibited phenotypic plasticity in their immune system profile and antioxidant expression (Migliaccio et al. 2019). A physiological systems analysis revealed that the immune cells, the sentinels of environmental stress responses in sea urchins, had an altered proteomic profile in the vent urchins. Plasticity of the sea urchin immune system may facilitate success under acidification. The eggs of *A. lixula* from a vent site, but not those of individuals from nearby ambient pH conditions, have a jelly coat that is more resilient to acidification, indicating plasticity in oogenesis to maintain gamete function in low pH (Foo et al. 2018b).

These studies highlight the potential for traits across physiological systems (e.g., reproduction, immune, growth) to exhibit positive phenotypic responses to acidification. As the vents are open systems where populations receive gene flow from larvae generated in surrounding ambient conditions, it is unlikely that local genetic adaption has occurred. However, the vent environment is likely to exert strong selection on recruiting larvae and post metamorphic success, despite the potential for reduced genetic diversity (Lloyd et al. 2016).

Many laboratory studies have investigated the potential that parental exposure to acidification conditions during gonad development will improve outcomes for offspring (Table S1). For *Strongylocentrotus droebachiensis*, the progeny generated by parents exposed to pH<sub>NBS</sub> 7.7 for 16 months exhibited increased resilience to acidification (Dupont et al. 2013). Fecundity was also similar to controls. The gonads would have fully matured under experimental conditions, providing a better opportunity for the gametes to be ‘imprinted’ promoting beneficial anticipatory plasticity.

Conditioning of *Psammechinus milliaris* at pH<sub>NBS</sub> 7.7 for 10 weeks showed positive effects for progeny (Suckling et al. 2014). Surviving larvae were larger, indicating that they were better able to calcify in low pH conditions, but as a comparative ambient pH treatment was not included, it is not possible to interpret the extent of this positive response. The marked reduction in larval survival indicated deleterious effects. The short time that the adults were in treatments would not have allowed the gonads to mature in conditions with potential to generate negative effects. Following a 7-week adult conditioning of *Echinometra* sp. A in pH<sub>NBS</sub> 7.7, the larvae produced did not differ from those of control parents grown in the same conditions (Uthicke et al. 2013). Adult conditioning did not ameliorate the negative effects of acidification on larval growth, skeletogenesis, and abnormality. The conditioning period was likely too short to provide a beneficial outcome for progeny.

Parental conditioning, the temperature at which gametes develop, influences offspring thermal tolerance. The offspring of mothers that experience warm conditions during egg development perform better in these same conditions (Byrne 2011). The progeny of warm range edge populations are more tolerant of warm conditions than those from cooler climes (Byrne et al. 2011). For echinoderms with broad latitudinal ranges, populations may be sustained through recruitment of thermo-tolerant propagules (indicative of phenotypic plasticity) (Byrne et al. 2011, Harianto et al. 2018).

Studies involving long-term exposure of adults to increased temperature show that the metabolic rate increases up to the tolerance limits (Carey et al. 2016, Delorme & Sewell 2016, Harianto et al. 2018). A 14-week exposure of *Helicidaris erythrogramma* to a range of temperatures (+2–6°C) showed that this species maintained physiological balance at moderate warming (+2°C) with high survival, while +4°C resulted in higher metabolic rates (Harianto et al. 2018, 2021). Similarly, *Evechinus chloroticus* held at +4°C for 6 weeks had increased metabolic rate, reduced growth, and reproductive failure (Delorme & Sewell 2016). Conditioning of *Strongylocentrotus intermedius* at +3°C for 3 months resulted in decreased hatching and smaller larvae (Zhao et al. 2018c). The gametes are unlikely to have imprinted to the offspring environment.

Habitat heating appears to be the contemporary climate change stressor of greatest concern, especially during marine heatwaves. Many echinoderms live close to their upper thermal limits (Delorme & Sewell 2016, Brothers et al. 2016, Vergara-Amado et al. 2017, Collin et al. 2018, Harianto et al. 2018, 2021, Gall et al. 2021, Minuti et al. 2021). While exposure of adult *H. erythrogramma* to heatwave conditions had a beneficial influence on larval development, there were negative carry-over effects for the resulting juveniles, with higher mortality of the juvenile offspring of parents exposed to heatwave conditions (Minuti et al. 2022). There is a tight relationship between spawning, temperature and photo-period/food availability for echinoderms (Reitzel et al. 2014) and so OW/heatwaves are likely to cause a mismatch between spawning and optimal conditions for larvae.

Conditioning of *Sterechinus neumayeri* in control, warm (+1.5°C), and two acidification-warming treatments (pH<sub>NBS</sub> 7.7/+1.8°C, 7.5/+2.1°C) for 17 months had positive outcomes for offspring (Suckling et al. 2015). The urchins maintained at pH<sub>NBS</sub> 7.5/+2.1°C had the largest eggs. This change was suggested to indicate higher investment to offspring under a warming scenario, a beneficial outcome. There was a trade-off, however, in higher larval abnormality, but no difference in the larval size indicating that adult conditioning in warm-acidification conditions ameliorated the negative effects of acidification on larval growth. This is likely due to +2.0°C countering the stunting effect of acidification on calcification in *S. neumayeri* (Byrne et al. 2013b). With the 17-month adult conditioning time, the gonads would have fully matured in the future offspring environment, promoting some beneficial outcomes.

*Helicidaris erythrogramma* maintained in multistressor OA and OW treatments over the entire gametogenic cycle with a seasonal offset for temperature (+2°C) and the seasonal photoperiod produced juvenile offspring with a higher metabolic rate (Harianto et al. 2021). It is not known if this response is a positive or negative outcome.

In a study where *Tripterus gratilla* was reared from the juvenile stage to maturity in present day, acidification (pH 7.6, pH 7.8), warming (+2°C), and OA+OW treatments, the gametes of these F<sub>0</sub> parents were used to produce F<sub>1</sub> progeny reared in the same conditions in a

crossed design (Dworjanyn & Byrne 2018, Karelitz et al. 2019). OA and OW significantly affected growth of the F<sub>0</sub> generation. They grew more slowly at pH 7.6, but not at pH 7.8. The urchins and their gonads were larger at the higher temperatures and warming offsets the negative effects of acidification (Dworjanyn & Byrne 2018). Despite their larger ovaries, the eggs of females raised at +2°C were up to 21.8% smaller than those of ambient females, indicating selection for maternal fitness over reproductive investment. This change may have influenced F<sub>1</sub> generation size.

With respect to the F<sub>1</sub> offspring, larval growth was affected by the interaction between temperature and pH with responses depending on parental environment. Larvae from control parents raised in ambient conditions were larger than larvae from any other parent/offspring treatment group, indicating a negative transgenerational effect. The progeny of parents reared to maturity in warming and OA+OW treatments exhibited a greater thermal tolerance and those of parents acclimated to OA had greater acidification tolerance.

There was some indication of an adaptive response. Larvae from ambient parents were smaller if reared in OA, OW, and combined stressor treatments. Larvae from acidification parents that were also reared in acidification were similar in size in each treatment, and they were not affected by reduced seawater pH or warming. For larvae from parents raised in the warm conditions, acidification significantly reduced growth, but there was no significant effect of warming. Larvae of the OA+OW parents were larger in warm treatments compared to larvae from the same parents raised in warm conditions only. These larvae also did not show reduced growth in response to acidification.

Larval morphological traits clustered according to parent source indicating that the environmental history of parents was the dominant factor, with offspring treatment playing a secondary role. Overall, despite some indication of beneficial effects, larvae of control parents raised in control treatments were larger in all traits measured than larvae of parents acclimated in warming, acidification, or both. Larvae from warm treatment parents were smaller than those from the other parental/offspring treatment groups, potentially due to decreased egg size. This study highlights the complexity of TGP and the importance OW and OA on marine animals.

In scenario-based studies, adult *Echinometra* sp. were maintained in ambient and two future climate scenarios (+1°C/685 ppm CO<sub>2</sub>, +2°C/940 ppm CO<sub>2</sub>) superimposed with seasonal fluctuations for 20 months to condition the gonads (Uthicke et al. 2020, 2021). With this experimental design, it is not possible to tease out the impacts of OA and OW as individual stressors. The gametes were used to generate F1 offspring. The larvae of the +2°C/pH 7.8 parents were the largest and had the highest respiration rates. Overall, there was decreased survival in the progeny of the parents from the two scenario treatments, indicating negative carry-over effects (Karelitz et al. 2020). The larvae that did develop did not differ in size across parental treatments (control and two scenarios) (Uthicke et al. 2020). The resulting juveniles were then reared for 25 months in experimental conditions and their growth and physiological parameters were measured (Uthicke et al. 2021). The urchins from the future scenario treatments experienced greater mortality, had depressed metabolism, and had decreased spawning capacity. Negative parental effects indicated little scope for transgenerational acclimation. For the crown of thorns starfish, parents in warm (+2C) and low pH (7.75) conditions for five months produced offspring with a higher survival rate than the wild type under these conditions indicating the potential for TGP (Hue et al. 2022).

### *Polychaetes*

Polychaetes are dominant both in terms of diversity and abundance in marine benthic communities from intertidal to abyss, as well as in estuarine and protected bays. Some polychaetes as adults are sedentary species living in tubes made of sand grains or calcium carbonate, while others move

freely within the sediment. Many polychaetes have mass spawning events restricted to 1 or 2 days of the year and their gametes are released into the water column where fertilisation occurs resulting in pelagic larvae which may spend hours to weeks in the water column allowing for dispersal of larvae to distant sites (Jamieson et al. 2006). Changes in ocean currents may transport larvae away from suitable settlement sites and increased run-off from storms may result in changes in salinity and turbidity which can impact juvenile survival, growth, and maturation (Qiu & Qian 1998).

In the limited number of polychaetes studied, OA interferes in the formation of the calcareous tubes of serpulids as well as weakening existing tubes (Wood et al. 2008, Smith et al. 2013, Li et al. 2014). This potentially makes them more vulnerable to predators and storm damage. Laboratory studies showed that increased acidification (pH 7.6) impacted the progeny of the invasive serpulid *Hydroides elegans* and that larvae had delayed metamorphosis as well as growth rates, confirming transgenerational responses (Lane et al. 2015). Another invasive serpulid species when raised in increasing levels of acidification exhibited smaller trophophores and built shorter and more fragile tubes when raised at pH 7.4, although settlement rates were similar to those found in the field (Díaz-Castañeda et al. 2019). Thus, increased acidification will lead to losses of reefs built by gregarious tube building serpulids, which create habitat for many other invertebrates leading to restructuring of communities that depend on these ecosystem engineers (Poloczanska & Butler 2010). Oysters subjected to elevated temperatures and changes in OA that disrupt the mineralisation of their shells will be subject to higher rates of infestation by boring polydorids increasing the mortality of the molluscs and reducing their commercial value (David 2021). This is an example of adaptation whereby the polydorids benefit from reduced shell strength of the oysters. It has been suggested that polychaetes living in volcanic habitats which are brooders or direct developers exhibit a pre-adaptive trait to enhance survival in such acidified waters (Lucey et al. 2015). Some evidence that a sabellid can adapt to increased acidification by reducing its body weight compared to animals living in normal seawater (Del Pasqua et al. 2019). As the cues to spawn for many polychaetes are related to changes in water temperature, any increases due to climate change almost certainly will impact on spawning and likely to produce pelagic larvae out of sync with food supplies (Olive 1995, Bates 2005).

Trans- and multigeneration studies with respect to climate change have largely been focused on one polychaete species, *Ophryotrocha labronica* (from the Mediterranean). This cosmopolitan invasive species occurs in fouling communities (Massamba-N'Sial et al. 2012). This small species which is easy to rear in the laboratory with a short generation time (17 days), weekly production of egg masses, and parental care is a good model for multigenerational studies (Chakravarti et al. 2016). Parental care is provided throughout development by swimming through the egg mass ensuring a constant supply of oxygen and preventing parasites from growing on the egg mass. Studies showed that transgenerational exposure to OA and OW had negative effects on fecundity, egg volume, hatching success, and juvenile development (Chakravarti et al. 2016). Another study on a population of this species maintained for about 30 generations raised in fluctuating pH (NBS 7.4–8.4) and then exposed to unvarying pH 7.7 for a further six generations showed initial ( $F_1$ ,  $F_2$ ) negative effects of acidification. However, by  $F_3$ – $F_7$ , fecundity levels were restored, and offspring performance improved (Rodríguez-Romero et al. 2016). Later transgenerational studies were carried out by Gibbin et al. (2017a,b) who exposed individuals of this species for six generations to four experimental conditions including increased water temperatures (+3°C) and acidification (–0.4 pH). They found that this produced faster growing worms, which reproduce earlier, but were smaller in size and hence had a reduced reproductive output. Such multigenerational studies are rare. Subsequent studies by Jarrold et al. (2019) investigated transgenerational exposure. They transplanted progeny at generations  $F_3$ ,  $F_4$ , and  $F_5$  between control and ocean warming and acidification, but significant changes in the level of plasticity across generations were few. Only juvenile development rate under the combined scenario modified transplant effect across generations – suggesting that this trait evolves to an increase in plasticity – when transplanted back to control conditions. Adaptive plasticity was conserved in most

traits despite significant levels of selection and strong declines in individual fitness in multigenerational exposure. So, while this species has been used as a model system to investigate the impact of climate change stressors over generations, all of those studies were carried out on a laboratory population that was maintained for years over thousands of generations and fed spinach. Exactly how relevant this is to other polychaetes in the field is unclear which suggests that all of these data should be treated with caution.

### *Crustaceans*

Crustaceans are a highly diverse group of economically and ecologically important species which play critical roles in trophic energy transfer. Crustaceans are expected to be tolerant of OA and OW due to their ability to buffer acid-based changes via the accumulation of bicarbonate as a buffer when challenged by reduced pH (Truchot 1979, Pane & Barry 2007, Pörtner et al. 2004) and lack of intensively calcified skeletal structures (Whiteley 2011). Pane and Barry (2007) found that while a shallow-water crab *Cancer magister* can compensate to short-term hypercapnia-induced acidosis, a deep water species *Chionoecetes tanneri* cannot compensate. It is suggested that deep-sea animals are adapted to a stable environment and have reduced metabolic rates compared to shallow-water species, and that their sequestration in oxygen-poor areas of the ocean would be detrimental to deep-sea fauna.

Copepods and amphipods with chiton-dominated skeletons are less sensitive to OA than lobsters with more heavily calcified skeletons (Whiteley 2011, Wang et al. 2018). With relatively short life cycles, i.e. days to months, crustaceans serve as a model to study trans- and multigenerational plasticity response of marine animals to climate change (Byrne et al. 2020, Table S1).

In the ecologically important amphipod *Gammarus locusta*, there was a strong negative transgenerational effect of acidification with 10–15% decreased survival and reproductive fitness (Borges et al. 2018) and reduced hatching success (Cardoso et al. 2018) because of increased oxidative stress (Lopes et al. 2019). When brooding females of *Sunamiphitoa parmerong* were maintained in ambient and warm conditions through progeny development and F1 rearing, the warm conditioned line had greater thermal tolerance (Campbell et al. 2020), but a multigenerational study found that while warming had no effect on F1 development, it increased F2 brood number, with the magnitude of change depending on diet (Ledet et al. 2018).

The prevalence of hypoxic areas in coastal waters is predicted to increase as a result of increased anthropogenic nutrient input and climate change (Bijma et al. 2013, Gobler & Hannes 2016). While many adult stages of estuarine invertebrates can cope with short periods of hypoxia, it is unclear if animals bred and reared in such conditions have this ability. Experiments using the estuarine amphipod *Gammarus chevreuxi* found that moderate hypoxia has markedly different effects as to whether adults exposed to short-term hypoxia or if they undergo their whole development under these conditions (Truebano et al. 2018). If these results are transferable to other estuarine species which are currently considered as hypoxia tolerant and given that hypoxia is predicted to occur frequently in coastal waters, this may have significant impact on the resilience of these animals which play an important role in estuarine ecosystems. Subsequent studies by Collins et al. (2022) investigated whether thermal acclimatisation impacted the ability of coastal amphipods to withstand hypoxia. Four closely related amphipod species were subjected to different temperatures and the species varied in their responses to temperature and hypoxia. Such studies using more than one stressor are critical in understanding how amphipods will react to changing conditions.

Transgenerational responses of copepods to acidification have been found to be highly species specific (Lee et al. 2020). Transgenerational studies of OA report decreased hatching success and offspring development in *Acartia bifilosa* and *Acartia tonsa* (Cripps et al. 2014). However, after 80 generations (3.5 years), beneficial acclimation responses to OA were not observed in *A. tonsa* (Langer et al. 2019) leaving behind a legacy of reduced developmental rate but not hatching

success. In *Acartia* sp., there was a positive transgenerational response from parents to offspring within a generation with significantly increased antioxidant capacity which mitigated biochemical damage caused by acidification and ultimately increased reproductive output (Vehmaa et al. 2016). Most recently, a study on the TGP over 25 generations of *A. tonsa* exposed to OW and OA found decreased thermal performance (deMayo et al. 2021). For *Pseudocalanus acuspes*, multi-generational exposure to acidification resulted in decreased fecundity in the F2 and reduced gene expression, including downregulation of RNA transcription genes (Thor & Dupont 2015, De Wit et al. 2016). For *Calanus finmarchicus*, the effect of OA on development of the F1 depended on acidification level (Pedersen et al. 2014).

Benthic copepods like *Tigriopus californicus* have shown little or no capacity for transgenerational acclimation and/or adaptation to warming even after 10 generations (Kelly et al. 2012). The lack of adaptive capacity may be explained by the low genetic diversity and poor acclimatory capacity associated with living in extreme habitats such as high intertidal areas (Somero 2010, Kelly et al. 2012, 2016). For *Tigriopus japonicus*, OA had no effect on hatching in a transgenerational study (Kita et al. 2013) or on embryo survival and larval production in a multigenerational study (Li et al. 2017). Recently, negative transgenerational effects of acidification in the harpacticoid copepod, *T. japonicus*, have found that glutathione peroxidase and superoxide dismutase may be partially responsible for decreased reproduction (Lee et al. 2019). In another benthic copepod, *Tisbe battagliai*, exposure to OA conditions in F3 resulted in negative effects on larval size and production as well as changes to the exoskeleton (Fitzer et al. 2012). A later study by Fitzer et al. (2013) again using *Tisbe battagliai* investigated their response to elevated  $p\text{CO}_2$  and environmental copper over two generations. They found that ocean acidification will enhance copper bioavailability resulting in larger but less fecund individuals, which may have an overall detrimental impact on copepod populations, an integral component of meiofaunal communities.

Parents of a shore crab exposed to warming mitigated the negative effects of other stressor (i.e., salinity) on the next-generation offspring, but such positive carry-over effect was highly variable (Torres et al. 2020).

Sessile barnacles are largely unaffected by OA and/or OW (McDonald et al. 2009, Pansch et al. 2012, Nardone et al. 2018, Campanati et al. 2016). In the subtidal barnacle *Striatobalanus amaryllis* and the intertidal barnacle *Amphibalanus amphitrite*, there was a positive transgenerational response to warming within two generations; however, the survival and acclimation response decreased in F2 compared to F1 (Morley et al. 2017).

### Corals

It is widely accepted that anthropogenic impacts, particularly global warming and OA, are two of the greatest threats to the future of coral reefs (Hughes et al. 2018, Perry & Alvarez-Filip 2019, Woodhead et al. 2019). Water temperatures that are only 1–2°C above normal summer maxima result in mass coral bleaching and extensive mortality (Ainsworth & Brown, 2021). Evidence also suggests that temperature and  $\text{CO}_2$  interact synergistically to increase the rate and severity of coral bleaching on reefs (Veron et al. 2009, Anthony et al. 2011, Putnam et al. 2017). The resilience of corals and coral reefs to climate change impacts depends on the responses of both the coral animal (host) and its endosymbiotic dinoflagellate partner (Ainsworth et al. 2010). Understanding the capacity, benefits and costs, of phenotypic plasticity through acclimation, acclimatisation, and adaptation of the symbiosis is a critical aspect in understanding resilience (Putnam et al. 2012). A recent review by Brown and Barott (2022) highlights the need to obtain a far better understanding of the acclimatisation versus sensitivity trajectories of a wide range of coral species to identify whether changes in bleaching susceptibility are related to physiological acclimatisation and/or trade-offs with other biological processes.

The acclimatory potential of corals to OA varies substantially among different Scleractinia growth forms. In some examples, branching corals exposed to lower pH have been shown to increase skeletal macro-porosity and growth by linear extension at the potential cost of weaker skeletal structures and increased fragility (Tambutté et al. 2015). In contrast, for slower growing mound-form coral species, OA has been linked to a decrease in calcification rates (Crook et al. 2013) and is unlikely to overcome the impacts of local OA. Putnam et al. (2020) investigated two distinct coral species, ‘sensitive’ *Pocillopora damicornis* and ‘robust’ *Montipora capitata*, experimentally exposed to a gradient of pH conditions. The environmentally resistant montiporid corals were found to either acclimate quickly or be buffered from the impacts of lowered pH, with no differences found in metabolic performance, DNA methylation, or calcification. In contrast, Putnam et al. (2020) found reduced calcification and changes to metabolic performance and DNA methylation in the more sensitive coral *P. damicornis*. As such, the authors concluded OA triggers phenotypic plasticity in corals potentially driven by DNA methylation in susceptible species and linked to plasticity in the juveniles. Jury & Toonen (2019) found that three coral species from Kaneohe Bay (Hawaii), which are naturally subjected to decreased pH and high temperatures, were more resilient to acidification and OW than conspecifics from a nearby control site, indicating the potential for corals to adapt to their environmental conditions. Similarly, *Stylophora pistillata* from the Gulf of Aqaba (Red Sea) are resilient to projected OA conditions (Bellworthy et al. 2019a,b).

There is some evidence to suggest that transgenerational tolerance to acidifying ocean conditions can occur in some coral species (Liew et al. 2018). In fact, Putnam et al. (2020) suggest that corals with the larval brooding life history have the most potential for transgenerational changes in tolerance to OA. Liew et al. (2020) challenge the concept that inheritance of phenotypic traits is solely via genetic means. They found that the inheritance of DNA methylation patterns provides a potential pathway for environmentally induced phenotypes which can contribute to evolution of species and populations. This suggests that there is a significant role of DNA methylation in intergenerational inheritance of traits in corals, which may enhance their capacity to adapt to climate change.

The capacity of corals for asexual reproduction and the spread of genotypes within a reef habitat through asexual reproduction is also a consideration in the success of adaption and acclimatisation (Willis et al. 2006). Recent studies further highlight the importance of the rate of change and the variance of exposure on the capacity for coral species to adjust performance while maintaining skeletal growth (Perry & Alvarez-Filip 2019).

As rapid coral growth (skeletal extension) is reflective of the success of the coral endosymbiosis, it is also important to consider the impacts of OA on the coral meta-organism given the documented impacts of OA to coral growth (Van Oppen et al. 2015, Putnam et al. 2017). Impacts to skeletal structure and function emerge as the most widely occurring alterations caused by OA, which are likely to be a challenge for acclimatisation and adaption to overcome when combined with the impacts of rising temperatures and storm intensity on coral reefs.

OW-driven coral bleaching is considered the greatest threat to the long-term sustainability of coral reefs worldwide. Bleaching events are caused by sustained SST. Increases of just 1–2°C above long-term summertime averages and the response of the corals’ endosymbiotic algae to warming define the bleaching response (Glynn 1993, Hoegh-Guldberg 1999). Ocean temperatures are predicted to rise approximately 1–2°C within this century, leading to near the now-realised near-annual mass coral bleaching events (Hoegh-Guldberg 1999, Parry et al. 2007). Over the past two decades, ocean temperatures have increased over 0.3°C on coral reefs and research has shown that a 0.5°C temperature increase is the difference between corals undergoing a survivable endosymbiosis breakdown and coral mortality (Fordyce et al. 2019, Leggat et al. 2019). As such, the coming decades are now considered the critical time for coral’s capacity to acclimate and adapt to the impacts of OW (Hoegh-Guldberg 1999, Hughes et al. 2003, Palumbi et al. 2014).

Coral species are often categorised by traits such as thermal tolerance, with some species known to be tolerant to increased temperatures and other coral species known to be susceptible (Carturan et al. 2018, Zawada et al. 2019). The corals endosymbiotic dinoflagellate (Family Symbiodiniaceae) also influence host resilience; corals hosting endosymbiotic algae previously designated as clade D symbionts are more thermally tolerant, while those corals hosting populations dominated by endosymbionts of clade C are typically growing faster and highly susceptible to warming water (LaJeunesse et al. 2018, Stat et al. 2013, Wong et al. 2021).

The dominant Symbiodiniaceae strain can radically influence the phenotype of the meta-organism, but there are trade-offs for the host coral and the symbiosis can be inflexible within some species thereby not conferring long-term resilience. The short generation time (3–10 days) of Symbiodiniaceae highlights the potential to increase their thermal tolerance in ecologically relevant time scales through acclimatisation and/or adaptation. However, the extent to which Symbiodiniaceae phylotypes can acclimatise or adapt and the potential flow-on effects on the stress tolerance, growth, and survival of the meta-organism are not well known. Experimental evolution approaches aim to determine if selection for resilient meta-organism structures and host phenotypes is possible (Torda et al. 2017). While there is some evidence that transgenerational adaptation, through DNA methylation, histone modification, or other mechanisms, can result in the rapid phenotypic acclimatisation of the coral host to temperature (Liew et al. 2020) and that Symbiodiniaceae in culture can increase their thermal maxima (Chakravarti & Van Oppen 2018), results using experimental adaptation in an intact holobiont have been mixed (Quigley et al. 2020a,b). Buerger et al. (2020) suggest that phenotypes seen in cultured algae may not produce similar tolerant phenotypes in the intact symbiosis.

Growth and survival of reef building corals is influenced by their symbiotic algal partners (*Symbiodinium* spp.). Cunning et al. (2015) addressed this by studying *Pocillopora damicornis* with either thermally sensitive (clade C) or tolerant (clade D) symbionts at various temperatures over many weeks. While warming waters will negatively impact corals, the clade of symbionts may affect their growth, highlighting the need to better understand such genotype–environment interactions.

A transgenerational selection study investigated experimentally induced thermal tolerance in thermally sensitive endosymbionts, *Cladocium goreau*, and it was found that heat tolerance had improved, but coral growth and survival had not (Quigley et al. 2021). Other studies of experimental evolution of Symbiodiniaceae have found that species can show signs of both improved thermal tolerance and capacity to confer improved thermal tolerance to the host coral (Buerger et al. 2020). Due to the long generation time of the coral host, studies have yet to determine if experimental evolution of the meta-organism improves thermal tolerance and survival under bleaching conditions. A recent study using the model *Aiptasia* found that while plasticity to stress was possible in endosymbionts, there was no evidence for conferred resilience, through symbiont exchange (Herrera et al. 2020), suggesting that there may potentially be species-specific limitations to organism adaptation. Experimental approaches involving reciprocal transplantation of multiple genotypes have provided promising results, suggesting that both genotype and environment selection are likely critical factors for the success of assisted acclimation and adaptation (Drury & Lirman 2021).

OW and OA also interact synergistically to decrease thermal bleaching thresholds, and species-specific thermal tolerance also influences organism capacity to withstand the impacts of OA (Anthony et al. 2008). The complex interplay of OA and OW from a genetic to organismal level, as well as the rate and cumulative environmental changes, is therefore a key factor in determining the ability of different coral species, and ultimately coral reefs, to be resilient under future climate scenarios.

### Marine fish

In general, fish are found to be relatively tolerant to CO<sub>2</sub> levels expected by the end of the century, due to their well-developed capacity for acid–base regulation (Brauner et al. 2019). The sensitivity of marine fish to OA is varied, with differences observed between species that are closely related or species that co-exist in particular habitats, as well as diversity in sensitivity between life stages within a species (Cattanoo et al. 2018, Munday et al. 2019). In some instances, the effects of elevated CO<sub>2</sub> have been positive, with enhancement of reproductive capacity at 584–1023  $\mu\text{atm}$  for the cinnamon clownfish (Miller et al. 2012). The strongest negative results have been observed during early life when acid–base regulation is not well developed (Ishimatsu et al. 2005), as well as on anti-predator response and behaviour (Munday et al. 2009, Dixson et al. 2010, Cripps et al. 2011). Consequently, these traits are commonly the focus of research into acclimation and adaptation (Table S1).

There is high capacity for phenotypic plasticity of physical traits to elevated CO<sub>2</sub> within only a few generations. Specifically, the negative effects on early development and survival have been restored with parental or multigenerational exposure in a number of species (see Table S1, e.g., *Menidia menidia*, *Amphiprion melanopus*, and *Gadus morhua*). In these studies, the exposure of adults during reproductive windows results in offspring that have enhanced or restored performance (e.g., growth, survival) in the same elevated CO<sub>2</sub> conditions. There are some cases where parental exposure has amplified the negative effects of CO<sub>2</sub> on offspring (Schade et al. 2014), not all traits measured have been restored (McMahon et al. 2019), or beneficial parental effects have been offset when developing with limited food (Stiasny et al. 2018). In contrast to the high plasticity of physical traits, there is limited evidence of acclimation in behaviour to OA (Welch et al. 2014, Welch & Munday 2017, McMahon et al. 2018). In cases where early life (Lopes et al. 2016) or parental exposure (Allan et al. 2014) has induced acclimation, only partial restoration has occurred. The limited rapid plasticity may be due to acid–base regulation causing interference with neuroreceptors like the GABA-A receptor (Nilsson et al. 2012, Lopes et al. 2016). It should be noted that CO<sub>2</sub> plasticity research has yet to rear parental fish for entire generations (only adults for 6 months to 1 year), which may be required to induce multigenerational plasticity (Donelson et al. 2018).

Disparity in acclimation capacity of physical versus behavioural traits may be due to the genetic control and heritability of CO<sub>2</sub> sensitivity (Malvezzi et al. 2015, Welch & Munday 2017, Tasoff & Johnson 2019). The few studies that have explored heritable transmission of phenotypes across generations have found low to moderate levels for physical traits (mortality/survival h<sup>2</sup>: ~0.2, growth h<sup>2</sup>: ~0.1), but high heritability for behavioural traits (anti-predator response h<sup>2</sup>: ~0.6) (Table S1). It is often found that traits under selection in nature are not highly plastic. In most cases, heritability did not change with CO<sub>2</sub> exposure, except for the highly heritable anti-predator responses of the spiny chromis coral reef fish, which under elevated 754  $\mu\text{atm}$  CO<sub>2</sub> heritability was lost (Welch & Munday 2017). The mechanism for transmission of anti-predator responses in this species has been linked to expression of circadian rhythm genes (Schunter et al. 2016).

The ectothermic nature of fish means that physiological performance and cellular function is inherently linked with changes in environmental temperature (Fry 1971, Huey & Kingsolver 1989). Consequently, there has been a wealth of research over the years exploring the thermal sensitivity of marine fish (e.g., Roessig et al. 2004, Munday et al. 2008, Pankhurst & Munday 2011), which has led to generalisations at the ecosystem or latitudinal level. As with terrestrial ectotherms (Tewksbury et al. 2008), a consistent pattern of tolerance matching the historical range and variation in environmental temperatures experienced by a species or population is observed in marine fish, making tropical and polar species more sensitive to projected OW than temperate species (Comte & Olden 2017, Stuart-Smith et al. 2017). However, historical environmental variation can also alter resilience to future climate change due to its effect on genetic diversity and the capacity for phenotypic plasticity (Scheiner 1993, Seebacher et al. 2005).

Within-generation thermal acclimation capacity in temperate and polar species is generally high, with acclimation possible with relatively short exposure lengths (e.g., days to weeks) and the flexible timing of thermal exposure within a life cycle (Table S1). Rapid acclimation has been observed in traits including growth (Mascaró et al. 2019), cardiovascular and metabolic physiology (Healy & Schulte 2012a, Safi et al. 2019), escape performance, and swimming ability (Temple & Johnston 1998). Comparatively, tropical marine fish seem to require longer exposure (i.e. months to year(s)) and/or exposure during early life (i.e., developmental plasticity, Nilsson et al. 2009, 2010, Donelson et al. 2011). In addition, within-generation thermal acclimation in tropical species often only partially compensates negative thermal effects (Donelson et al. 2011) and does not occur at all thermal exposures (Grenchik et al. 2012). In some cases, thermal exposure produces greater impacts on performance than acute thermal testing (barramundi: Norin et al. 2014, wrasses: Motson & Donelson 2017).

The most common trait tested across species has been critical thermal maximum, perhaps in part due to ease of measuring. Critical thermal maximum also shows a similar pattern, where the majority of temperate and polar species increase maximum tolerance similar to the rate of thermal change, but tropical species have limited plasticity (Table S1). Only Habary et al. (2017) found high capacity for the reef damselfish *Chromis viridis* to increase thermal maximum ( $\sim 1^{\circ}\text{C}$  per  $2^{\circ}\text{C}$  acclimation temperature increase). Comparisons of thermal maxima should be made cautiously, as uniform rates of change across studies are not employed, and in many cases, warm acclimated fish begin thermal testing from a higher starting temperature, thus making disentangling acclimation from starting temperature difficult. Whether critical thermal maxima are useful in predicting thermal resilience of fish, as other traits suffer many degrees below, is often questioned.

Studies investigating multigenerational plasticity highlight the large potential role it will play in the resilience of marine fish to warming, as it generally enhanced or restored performance above what occurred from within-generation plasticity (Donelson & Munday 2012, Donelson et al. 2012). Yet it also highlights the complexity of predicting responses in nature, with varying results between rapid or increment warming (Donelson et al. 2016) and differences across experimental generations (Shama et al. 2014, 2016). In addition, research on the sheepshead minnow highlights that either exposure length or timing during parental reproductive cycle may be critical to induce TGP in offspring as beneficial effects were only observed with a 60-day exposure rather than a 30-day exposure (Salinas & Munch 2012).

Technology developments have allowed exploration of the potential underlying genomic mechanisms driving within- and multigenerational thermal plasticity, which has largely been explored with transcriptomic analysis. Across the species studied so far, expression changes have been seen in genes involved in metabolism, mitochondrial activity, mitochondrial respiration, tissue development, transcriptional regulation, immune response, and stress response occurred in response to warming (Veilleux et al. 2015, Shama et al. 2016, Bernal et al. 2018). Differential methylation has also been explored and shifts in methylation of insulin response, energy homeostasis, mitochondrial activity, oxygen consumption, and angiogenesis genes were correlated to plasticity of aerobic capacity (Ryu et al. 2018).

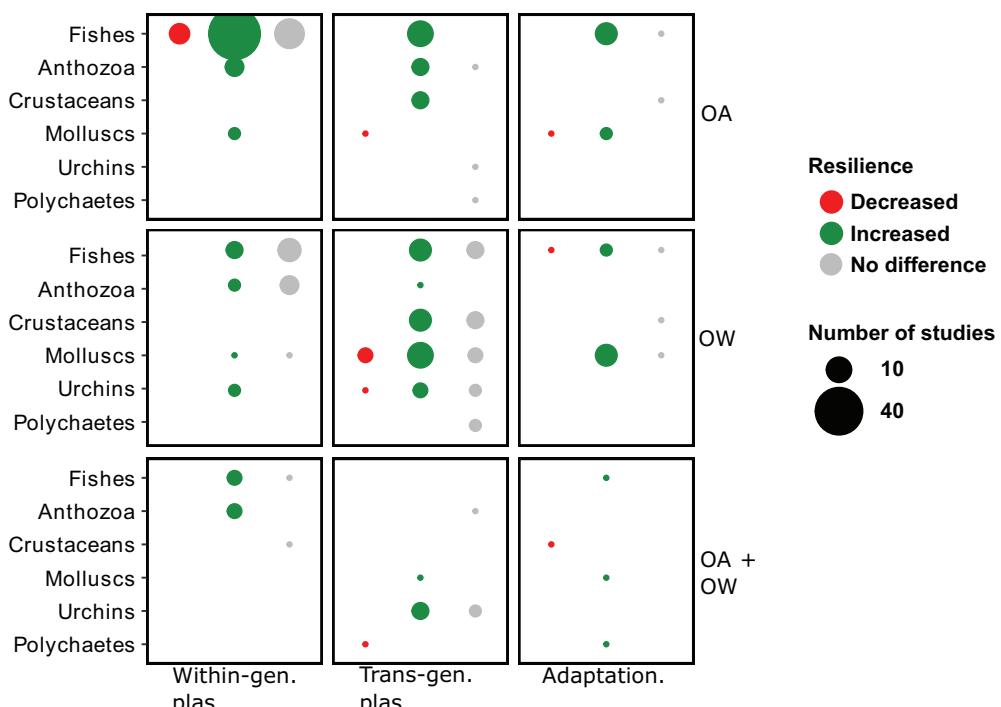
Far less research involving marine fish has focused on adaptation to OW, including understanding of local adaptation that may already exist in current populations as well as the capacity for adaptation to future change. This is likely in part due to the expectation that rapid climate change is occurring at a rate greater than selection and genetic adaptation to keep pace with for the majority of species (Chevin et al. 2010, Kopp & Matuszewski 2014). It is also likely to be linked to the challenges of studying adaptation in relatively long-lived species as it requires following numerous generations and ideally *in situ* where natural selection can occur. One such adaptation study, on Atlantic herring, has identified selection outlier loci that correlate with thermal and salinity environmental experience (Limborg et al. 2012). In a few laboratory experiments, adaptation has been explored through establishing the heritability of beneficially plastic traits (Munday et al. 2017) and gene  $\times$  environment interactions (Munday et al. 2017, Shama 2017). When explored, it is consistently found that certain genetic or family lines can outsurvive or outperform others, providing the opportunity for adaptation

in nature (Munday et al. 2017, 2019, Shama 2017, Zanuzzo et al. 2019). More research into understanding the interplay between plasticity and adaptation is especially pertinent because the adaptive nature of beneficial phenotypic change is generally assumed rather than proven.

## Challenges to resilience of marine animals

Considering the relatively recent emergence of OA, OW, and OD research, a lot has been done within a short time, although the impacts of increased temperature on marine animals have long been of interest (e.g., Review Byrne 2010). Challenges to resilience of marine animals in the Anthropocene are summarised below.

Many molluscs species may be lost over the coming decades. Studies suggest that molluscs have a capacity for phenotypic plasticity through the process of TGP which has been the most studied resilience mechanism and appears to ameliorate at least partially some of the negative effects of OA (Figure 1). How TGP responses will differ across populations and habitats, the longevity of TGP responses and the mechanisms underlying them and whether they come with trade-offs requires further investigation. Adaptation of molluscs via the selection of tolerant genotypes appears to be possible. This is based on a limited number of species, making it difficult to predict whether tolerant genotypes will be sufficient to prevent losses of mollusc populations and aquaculture industries. Selection of tolerant genotypes will likely be important to enhance food security and maintain economic benefits. Our understanding of the impacts of increase temperature on molluscs in the context of global change is poor, especially for populations living close to their thermal limit where resilience capacity may be reached. Considerably more research is



**Figure 1** Summary of marine animals' response to Ocean Warming (OW), Ocean Acidification (OA) or Ocean Warming and Ocean Acidification (OW+OA). Sizes of the points indicate number of studies for each taxa and colours indicate increased or decreased levels of resilience measured in those studies.

needed to understand the resilience response of molluscs to multiple stressors, i.e., OA, OW, and OD combined (Keppel et al. 2016).

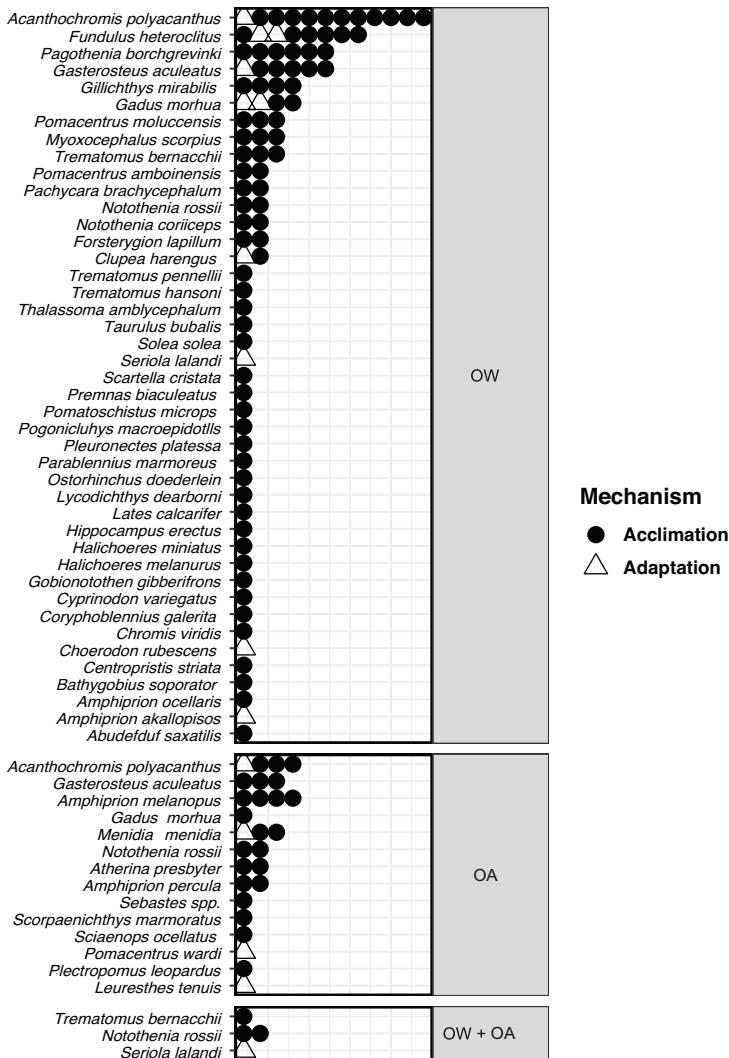
For echinoderms, while adaptive capacity and protective mechanisms have been much discussed, they remain to be demonstrated. Overall, many TGP studies on echinoderms show the importance of gamete development over the complete gametogenic cycle so that gonads fully develop and mature under experimental conditions, and this is likely to be associated with imprinting of the germ line (Byrne et al. 2020). The weight of evidence indicates that the effects on offspring depend on the OA and OW level and the duration of adult conditioning. It appears that phenotypic plasticity has some potential to mitigate the effects of changing climate on offspring fitness, but it is unknown if the beneficial traits can be maintained over generations. However, negative TGP to OA and OW were evident in many species. Some studies of sea urchins from upwelling and vent habitats indicate the presence of genetic variation in stress response mechanisms, the type of variation upon which selection operates. The presence of sea urchins that thrive under low pH sites or warm range edge conditions indicates considerable phenotypic plasticity and individuals with resilient genotypes. The impacts of OD and freshening on echinoderms in the context of global change (see Sato et al. 2018, Clements et al. 2022) are far less understood, leaving important knowledge gaps to address.

There have been very few studies on the phenotypic plasticity and adaptive capacity of polychaetes. Given that polychaetes have been around since the Cambrian and occupy all marine and estuarine habitats from soft bottom communities in the deep sea to the intertidal, they certainly have the capacity to adapt, but how quickly they can do this is unknown. Polychaetes exhibit a range of feeding habits and play an important role in the bottom of food chain with lifespans from a few weeks to years. So, while abundant as shown in Table S1, few species have been studied from only five families, including some invasive species.

This is regrettable given the positioning of polychaetes at the base of the food chain. Changes in species composition and abundance will almost certainly have flow-on effects on food chains in terms of the breakdown of organic matter and for those species which feed on polychaetes in the benthos and in the water column above. As many species can easily be maintained in the laboratory, they are good candidates for studying their adaptive capacity and their tolerance limits. Crustaceans unlike other marine organisms appear to have resilience, and the challenge of OA and OW is associated with physiological trade-offs.

Coral reefs have served as a model system for marine resilience being an ecosystem in crisis and at risk of being permanently lost. A range of human activities are threatening their capacity for persistence (Hughes et al. 2018). Hughes et al. (2010) outline that resilience of coral reefs is defined by non-linear (threshold) dynamics in response to slow and fast stressors which drive change, alternate persistent phases, reinforcing feedbacks, and hysteresis. TGP studies suggest that corals have the capacity to improve their resilience to OA, although this resilience appears to be species specific with some species more vulnerable than others. Understanding the capacity, benefits and costs, of plasticity, acclimation/acclimatisation, and adaptation of the symbiosis is a critical aspect in understanding resilience (Putnam et al. 2012). Other alliances such as coral chimerism (Rinkevich 2019) are largely understudied. The question of whether they will have resilience to the combined stressors of OA and OW and do this fast enough remains, given that so many corals are already living close to their thermal maxima and how climate change will interact to increase susceptibility of corals to disease (Maynard et al. 2015, Peixoto et al. 2017). Answering the fundamental questions of resilience and how corals and diverse coral reef ecosystems may acclimatise and adapt to OA and OW therefore requires an understanding of the genetic capability of potentially hundreds of habitat forming coral species and their meta-organism structure. Studies have also suggested that there will be a need to move beyond coral reef ecological theory to include human and socioeconomic and cultural processes if we are to successfully conserve corals in the Anthropocene, a time of rapid change (Williams et al. 2019).

For marine fish, at first glance, future resilience is looking relatively robust. Generally, there is good capacity for both acclimation and adaptation producing improved performance (Figures 1



**Figure 2** Number of studies that have investigated the resilience of marine fish to Ocean Warming (OW), Ocean Acidification (OA) or Ocean Warming and Ocean Acidification (OW+OA). Shapes indicate the resilience mode, either acclimation (circle) or adaption (triangle).

and 2). This perspective of high resilience in fish results from research on smaller bodied species that are amenable to experimental research and traits that are easily measured (Figure 2, Table S1). There is concern that resilience of aerobic physiology and critical thermal maximum may not translate to growth (Grans et al. 2014) and reproductive capacity (Donelson et al. 2016). Research so far has allowed us to understand the fundamentals of acclimation, adaptation, and even underlying genomic mechanisms (Table S1). However, for most of humanity, the main concern is the resilience of fishes that provide food security and livelihoods, for which there is a significant lack of knowledge. While a relatively large body of research compared to other marine taxa has been conducted (Figure 1), it still presents some limitations when predicting future resilience. First, there is a limited understanding of how the combination of OA and OW or OD will affect the resilience of marine fish. What we know from acute effects of these combined stressors (i.e., not testing for acclimation and adaptation) is that we often cannot effectively predict a multistressor response from the

individual single stressors (Nowicki et al. 2012, Ferrari et al. 2014, Sswat et al. 2018). Furthermore, all combination stressor studies on resilience employ a joint change in both temperature and CO<sub>2</sub>. However, with the continued occurrence of MHWs (Oliver et al. 2018), a sequential experience of temperature followed by CO<sub>2</sub> may be more realistic, but we lack an understanding of how this may shift the phenotypic plastic and adaptive responses. Another potential limitation is that while there is a wealth of experimental studies on plasticity, they have rarely been conducted to allow heritability and selection to be incorporated. As such, we cannot be sure that rapid resilience achieved in the laboratory will play out in nature once ecological processes take place (e.g., predation, competition, sexual selection). It is also worth noting that many fishes rely on habitat forming organisms like corals for survival or other taxonomic groups for food (Coker et al. 2014, Abrantes et al. 2015, Froehlich et al. 2022), and thus, the resilience of fishes cannot be considered in isolation.

One significant unanswered question is whether phenotypic plasticity of marine animals will be rapid enough to cope with the pace of anticipated climate change. For example, experiments repeating a study carried out 100 years previously have shown that an intertidal flatworm *Procerodes littoralis* has been able to undertake microevolution enabling them to adapt physiologically to changes in salinity over a 100-year period. Experiments conducted in 1914 were repeated in 2016 and 2017 to compare regeneration over a range of salinities (Clayton & Spicer 2020). These authors found that regeneration occurred over a wide range of salinities, whereas they had an optimum salinity (Salinity=25) in 1914. During these 100 years+, rainfall has increased and the species is subjected more often to freshwater as well as full strength seawater during the tidal cycle. This suggests that *P. littoralis* has the physiological capacity of these animals to heal themselves at low salinities and is adapted to living in hyposaline waters as well as being able to heal in these salinities.

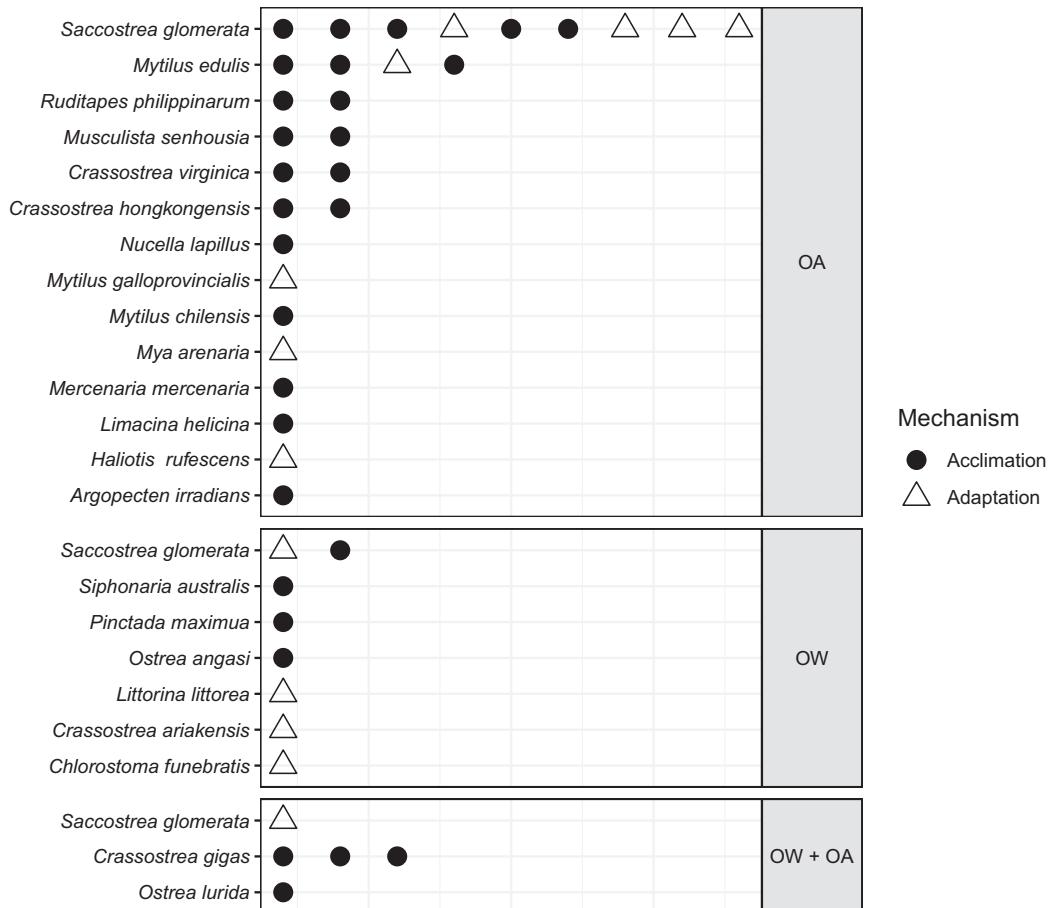
Although not an animal, studies have investigated the ability of diatoms, which contribute about 20% of global primary production, to adapt to global warming (Schaum et al. 2018) studies. Schaum et al. (2018) found that the marine diatom *Thalassiosira pseudonana* could adapt to rising water temperature if temperature increases slowly over time or where they fluctuate between benign and severe conditions, but have far less ability if the increases are rapid. They exhibit both major genomic and phenotypic plastic changes. They further suggest that carbon-use efficiency (CUE) in the warm-adapted lineages arise due to differences in temperature sensitivities of photosynthesis and respiration which are highly conserved metabolic highways and may be this could be universal across a broad diversity of phytoplankton. This will also assist in projecting marine primary productivity in the future.

### *Knowledge gaps/research needs*

Measuring resilience is a challenge because it requires controlled, ecologically and temporally relevant experiments that commensurate with the pace of projected changes. With gradual stressor introduction over longer experimental durations, the potential and limitations of adaptive capacity are becoming clearer.

Mechanisms of resilience require further investigation. So far, evidence suggests anticipatory changes in gamete development, particularly maternal effects through loading of cellular defences into the eggs such as heat shock chaperone proteins and epigenetic changes (Hamdoun & Epel 2007, Kanndorp et al. 2018, Eirín-López & Putnam 2019, Byrne et al. 2020). Transcriptomic changes have also been found and believed to alleviate the effects of apoptosis through cell cycle regulation (Goncalves et al. 2017).

Our knowledge of the resilience of marine animals to climate change is focused on certain model species because of existing genetic understanding, simplicity of husbandry, a well-known life history, or proximity to research facilities, for example, fish such as *Acanthochromis polyacanthus* and *Fundulus heteroclitus* (Figures 1–3). Also species like the oyster *Saccostrea glomerata* have been the focus of research for aquacultural and economic reasons (Figure 3).



**Figure 3** Number of studies that have investigated the resilience of molluscs to Ocean Warming (OW), Ocean Acidification (OA) or Ocean Warming and Ocean Acidification (OW+OA). Shapes indicate the resilience mode, either acclimation (circle) or adaption (triangle).

In summary, to date, we have limited understanding of the adaptive capacity and resilience of marine animals for several reasons.

First, most studies have done multiple studies on the same model species which are easily manipulated in the laboratory. While this comes with the benefits of species which can be easily kept in the laboratory for extended periods of time without significant mortality at multiple stages of their life history, it also creates a lack of broad representation of species responses in most groups and may not represent what is happening in the field or environment. The arguments about collapsing acclimation with acclimatisation will not lead to an understanding of mechanisms and responses which may vary depending on laboratory versus field conditions. For example, in echinoderms, most studies are on sea urchins and sea stars. In molluscs, most studies are done on bivalve oysters. In polychaetes, most species studied are on invasive and intertidal species. Rather than switch species, researchers seek to build on previous findings. This provides a sound base of knowledge of resilience for some species at the cost of a broader understanding of resilience which is exacerbated by a publication bias towards strong and significant results (Yang et al. 2022). This is despite multiple studies outlining the species-specific nature of climate change responses (Hoegh-Guldberg et al. 2018).

It is clear that investigations need to be expanded to incorporate more species from a variety of habitats and a broader representation within each group. This is needed because without broad representation of species, predictions about whether marine animals will have sufficient adaptive capacity and resilience is limited. A more deliberate and inclusive approach is also needed because most species tested so far, with the exception of oysters, are also not ones that human populations rely on for protein sources. Further, as many species studied to date are intertidal, they might have a more plastic response to environmental change and thus greater resilience; however, this might not be a representative response of those marine animals in more stable subtidal habitats.

Increasing representation, however, has the challenges of funding. Studies that broaden representation may involve species which might not be as amenable to manipulative experiments and come with increased risk and costs. Due to the difficulties in maintaining some groups of animals in the laboratory under experimental conditions, there is also a lack of multigenerational studies. Groups such as crustaceans some of which have short life-history times and are amendable to laboratory experiments are an exception to this. It is difficult, however, to extrapolate the findings from studies on crustaceans to other marine animals with calcium carbonate shells. Further, even when species are kept in the lab for multiple generations, in the case of one targeted polychaete species, they are fed on spinach, and this has no resemblance to what happens in the real world.

Second, our understanding of the resilience of marine animals to climate change is also limited because studies are mainly restricted to the impacts of single or combined OA and OW rather than the impact of multistressors. There is a dominance of research on single, rather than multiple stressors (Figure 1). Of the 208 studies considered in this review, only 17 (8%) investigated the combined effects of elevated temperature and CO<sub>2</sub>. Unlike these experiments, however, OA and OW will not occur in isolation (Lee et al. 2021) and combine with other environmental factors such as OD (Gobler & Hannes 2016, Sampaio et al. 2021) and extreme events such as MHWs and HEs (Sampaio et al. 2021).

More studies are needed which incorporate multiple stressors OA, OW, and OD including localised stressors such as water quality, salinity, harvesting, and pollution. Combined OA and OW stressors generally exhibited a stronger response (either positive or negative) effect (Harvey et al. 2013). Harvey et al. (2013) caution against drawing conclusions from single stressor experiments and also predict increased likelihood of stressors interacting and intensifying in the future. Recent results suggest that the interactions of multiple stressors are even more concerning. For example, Sampaio et al. (2021) found that hypoxic events elicited consistent negative effects relative to control biological performance – survival (~33%), abundance (~65%), development (~51%), metabolism (~33%), growth (~24%), and reproduction (~39%) – across the taxonomic groups (molluscs, crustaceans, and fish), ontogenetic stages, and climate regions studied. Once again, the reason for the absence of multiple stressor studies is because of the difficulties of these experiments which require considerable upscaling and cost. The benefits of multiple stressor experiments are a more realistic understanding of resilience of marine animals which enable adaptive planning. Multiple stressor studies need to be balanced with the need to investigate responses of marine organisms to acute events such as heatwave stress with realistic experimental heatwave scenarios and freshwater incursions with rapid drops in salinity and HEs (Sampaio et al. 2021). The effects of MHWs are a knowledge gap and there is the potential for the induced selection to shift population phenotypic and genetic structure to either enhance or hinder adaptation. Heatwave events and greater precipitation will become more frequent with climate change, and we need to know how marine animals will respond to these events. Further research is needed on the multiple climate change stressors which impact the resilience of marine animals.

Third, there is also no consensus even within well studied groups, such as fish, as to what are the key traits that determine resilience. The predictions of resilience are potentially biased by the traits that are chosen to be studied and there is even contention around the measurement of some variables such as cTmax in fish. This is a considerable challenge for the field because it is species and ecology specific. A solution to this and a way forward in resilience research is to create a guiding framework to allow enhanced comparative abilities. While concentrating research on select species can narrow our understanding of resilience, this can be alleviated with a trait-based approach for future research (Butt et al. 2022).

Finally, there is a need to go beyond single species studies to be able to predict marine ecosystem responses – for instance, a focus on climate change impacts on ecological influential interactions such as predator–prey relationships is required (Wright et al. 2014, 2018, Manríquez et al. 2021, McLaren & Byrne 2022). Since many of the investigated marine species are at the bottom of the food chain, their extinction may have major trophic flow-on effects.

## Conclusion/synopsis

This review has synthesised the literature on resilience to climate change of the main groups of marine animals. Marine animals are ecologically, economically, culturally, and aesthetically important, provide essential ecosystem services in coastal and estuarine environments, form the basis of aquaculture industries, and are a source of protein for humans across the globe. Whether marine animals will have the phenotypic plasticity and adaptive capacity to persist against multiple stressors remains unknown. Whether phenotypic plasticity will buy enough time for adaptation and evolutionary rescue and be fast enough to keep up with the rapid pace of climate change remains to be seen and a critical area of research (Byrne et al. 2020, Harmon & Pfennig 2021, Morgan et al. 2020). It is likely that for many marine animals, climate change will breach thresholds and create a tipping point in their resilience.

## Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

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**Supplementary Materials are provided online at:** <https://www.routledge.com/9781032426969>